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Kenneth J. Sulak
Florida–Caribbean Science Center Biological Resources Division, kenpsulak@nbs.gov

James P. Clugston
Florida–Caribbean Science Center Biological Resources Division

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Early Life History Stages of Gulf Sturgeon in the Suwannee River, Florida

KENNETH J. SULAK* AND JAMES P. CLUGSTON[1]

Florida–Caribbean Science Center
Biological Resources Division, U.S. Geological Survey
7920 Northwest 71st Street, Gainesville, Florida 32653, USA

Abstract.—Egg sampling confirmed that Suwannee River Gulf sturgeon *Acipenser oxyrinchus desotoi,* a subspecies of Atlantic sturgeon *A. o. oxyrinchus* use the same spawning site at river kilometer (rkm) 215 from the mouth of the river each year. Forty-nine eggs were recorded in 1995, and 368 were recorded in 1996. Spawning began 4–7 d after the March new moon in both years and lasted 10–11 d; in 1996, a second 10-d spawning round began on the April new moon. Developmental synchrony among eggs recovered suggested several discrete spawning events in both years. Total eggs deposited for three 1996 sampling days was estimated as 405,600–711,000/d, approximating the fecundity range of a large female Gulf sturgeon. Eggs were found only in the southern half of the river, an area with surface currents of 0.5–1.5 m/s and numerous eddies producing reverse bottom currents of 0.1–0.5 m/s. Egg substrate consisted of bedrock limestone thinly overlain by fine sand and densely distributed elliptical gravel 2–10 cm in diameter. Eggs were found predominantly in depths of 2–4 m at water temperatures of 17–21°C, conductivities of 50–100 μS, and dissolved oxygen levels exceeding 5.0 mg/L. The Cody Scarp, 15 rkm above the spawning ground, may mark the upstream limit of spawning areas in the river. Three 2–4-month-old riverine juveniles (82–115 mm total length, TL) collected are the smallest yet captured from any river. Data for 18 riverine age-0 juveniles (to 350 mm TL) suggest that this stage lasts 6–10 months, terminating with migration of fish to the river mouth in January–February. Less than 2% of 461 juveniles captured at the estuarine river mouth (1990–1993) were under 350 mm TL. Riverine age-0 fish were collected over long shallow stretches (typically <4 m deep) of relatively barren sand (rkm 12–238).

The Gulf sturgeon *Acipenser oxyrinchus desotoi,* a subspecies of the Atlantic sturgeon *A. o. oxyrinchus,* is federally listed as a threatened species. The Gulf sturgeon is anadromous, inhabiting Gulf Coast rivers from Louisiana to Florida. Spawning takes place in freshwater in the spring, but critical spawning habitat and early life history information is lacking. Random sampling with artificial substrate samplers in 1993 and 1994, yielding the first captures of Gulf sturgeon eggs, indicated that spawning occurs between river kilometers (rkm) 201 and 221 (zero reference: channel marker 21 at the mouth of the Suwannee River) (Marchant and Shutters 1996). In extending this 1988–1994 work, our objectives were to locate and characterize the physical and hydrological habitat conditions critical to Gulf sturgeon early life history stages.

Methods

A site located about 215 rkm upstream of the Suwannee River mouth and just above the confluence with the Alapaha River (Figure 1) yielded four Gulf sturgeon eggs in 1993 and 1994 (Marchant and Shutters 1996). In 1995, we employed a rectangular grid array of samplers and focused on a 1,500-m-long stretch of the river centered on rkm 215.5 (Figure 2). Based on these data, in 1996 we sampled 900 km of this area more intensively to home in on the center of the spawning ground (Figure 3).

In 1996 we also conducted exploratory sampling for eggs at rkm 93 (Figure 1). In both years, we used a multigear approach to search for riverine age-0 Gulf sturgeon from rkm 0 to 238 (Figure 1). In winter 1990–1993, we used gill nets to sample estuarine-stage juveniles at the mouth of the Suwannee River (Figure 1), primarily in the West Pass area (rkm 0–2.5).

Egg Sampling at rkm 215

Samplers were adapted from Marchant and Shutters (1996), and floor buffer pads were used as artificial substrates. Each sampler consisted of a circular pad (55.9-cm diameter, 0.25-m^2 upper surface area, 2.5 cm thick) deployed with a rebar grapple anchor and a hauling line to a numbered surface buoy. We used red pads to facilitate visual detection of the black eggs. Samplers were de-

* Corresponding author: ken_sulak@nbs.gov
[1] Retired.

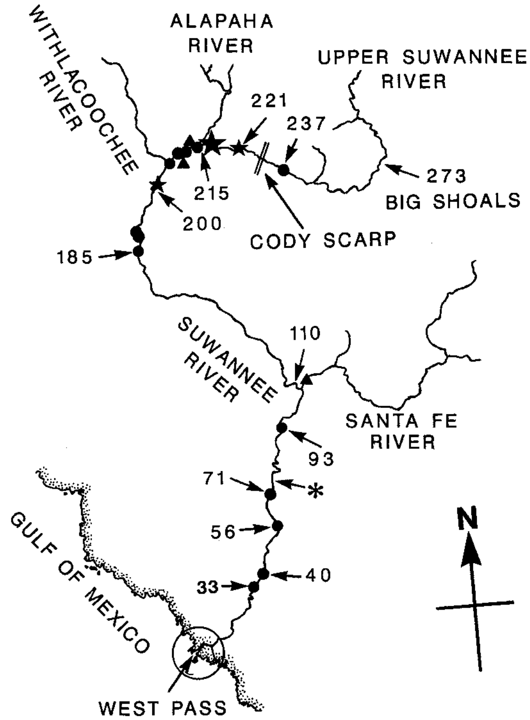

FIGURE 1.—Capture sites (1991–1996) for Gulf sturgeon early life history stages. Upriver distances are given as river kilometers (rkm) from the mouth of the river. Stars = egg collection sites; solid dots = our records of juveniles shorter than 450 mm total length; solid triangles = other juvenile records; circle denotes area of winter congregation of estuarine juveniles; asterisk indicates the upstream limit of tidal influence.

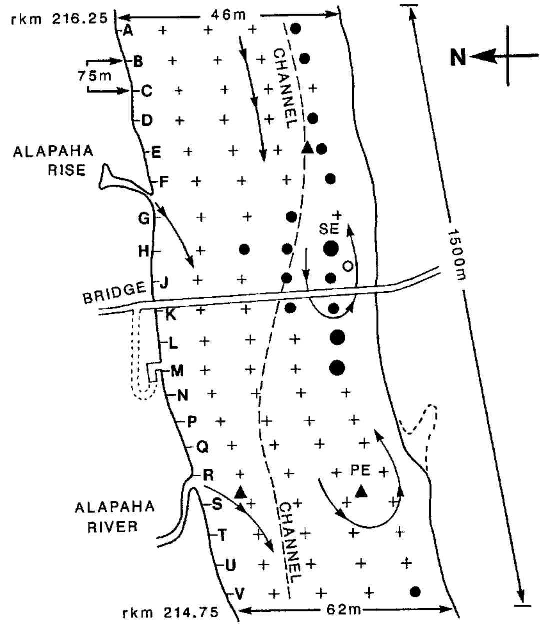

FIGURE 2.—Detail of 1995 egg sampler array at rkm 215. Illustrative key is as follows: crosses = positions of samplers; small solid circles = positions yielding a single egg only; large solid circles = samplers yielding eggs on multiple days; open circle = additional 1995 egg collection; solid triangles = 1993 and 1994 egg collection sites; dashed line = river channel; arrows indicate surface current direction; PE = permanent eddy; SE = seasonal eddy.

ployed in a fixed rectangular grid array. We used a nonrandom sampling design for logistic simplicity and to meet specific objectives: initially to (1) spatially identify and circumscribe the specific spawning ground, and (2) plot the pattern of occurrence of eggs recorded on samplers; and then to (3) define the physical and hydrological characteristics of the spawning ground, (4) determine the dispersion pattern of eggs deposited, and (5) estimate the number of eggs produced per spawning bout within the confines of the spawning ground.

1995 egg sampling.—In 1995, 80 samplers were deployed in 20 fixed transects over an area of 1,500 × 50 m (75,000 m^2), beginning 415 m above the Alapaha Rise (rkm 216.25). Four egg samplers were spaced equidistantly across each transect, resulting in a regular 20 × 4 grid array (Figure 2). Transect positions, denoted by alphabet letters, were marked along the north river bank with lettered survey flags; letters were also painted onto tree trunks.

Sampling was scheduled about every 48 h to enable detection of discrete spawning events, based on a predicted 85-h time to hatching at 18.5°C (Parauka et al. 1991). Thus, barring egg loss from pads, all adherent eggs should have been detected before hatching. On each sampling day, all 80 samplers were individually retrieved, examined for eggs, and redeployed in the same positions.

The 1995 array was deployed to coincide with the March full moon. But no eggs were collected and the array was redeployed on 28 March to span the 30 March new moon. Samplers were examined on 30 and 31 March and subsequently every other day through 21 April. Eggs collected were examined for stage of development and were either preserved in 5.0% unbuffered formalin to document developmental stage at time of collection, or were removed for laboratory incubation by excising a small portion of surrounding pad material with scissors. Voucher eggs were preserved to document species identification and cleavage stage.

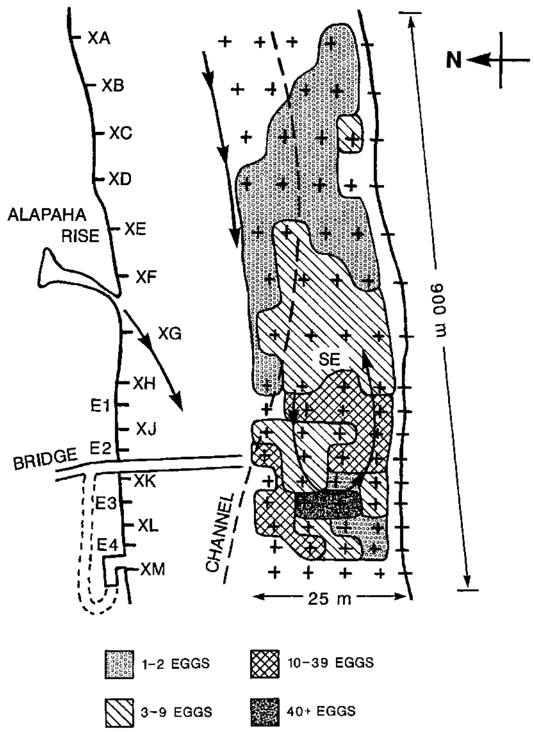

FIGURE 3.—Detail of 1996 egg sampler array at rkm 215. The prefix X denotes 1996 transects corresponding with 1995 transects (e.g., 1996 transect XA corresponds with 1995 transect A in Figure 2). Transects E1 through E4 represent additional 1996 transects. Symbols are as given for Figure 2. Shading denotes distribution of egg densities indicated by total eggs recorded by individual samplers; the 25-m scale indicates half the river width.

Each positive collection was accompanied by site-specific measurements of habitat characteristics, including surface and bottom water temperatures, dissolved oxygen, conductivity, and current velocity. Additionally, qualitative observations were taken on substrate type, submerged vegetation and the abundance of aquatic insect larvae (based on material adhering to or embedded within buffer pads).

Our intensive sampling was discontinued after 21 April. However, 20 samplers were redeployed, clustered within the identified center of egg deposition, to qualitatively monitor for any continued spawning activity and identify its cessation.

1996 egg sampling.—We confined our 1996 sampling at the rkm-215 site to 30% of the 1995 transect area (Figures 2, 3), focusing on the center of egg deposition along the southern side of the river. Forty-eight standard samplers were deployed (transects XA–XM; Figure 3). An additional set of 16 experimental two-layer samplers were also deployed in four rows (E1–E4; Figure 3). The overall grid covered an area of 22,500 m^2. Samplers were deployed on 29 February 1996, 1 d before the new moon; water temperature was 17.0°C. Samplers were inspected every third day until the first eggs were obtained, then at least every other day (daily from 28 March through 2 April) until apparent cessation of spawning on 4 April. After that, samplers were examined every third day until eggs were again detected on 17 April, and thereafter on 18, 19, 21 and 26 April. Samplers were removed on 7 May.

Twenty eggs were collected and preserved to document developmental stages and establish range in diameters of spawned eggs. Eggs were measured to the nearest 0.05 mm with an ocular micrometer. Otherwise, attached eggs were returned to the water on their sampler pads in the original sampler position. Eggs were categorized as either freshly spawned, ''black'' eggs (entirely black, early cleavage stages, 2.35–2.65 mm in diameter) or larger, at least 1-d old ''brown'' to ''yellow'' eggs (brown with yellowish developing animal pole, 2.70–3.35 mm in diameter).

On three sampling days, large numbers of eggs were collected on multiple samplers. For these days only, the dispersion among samplers of newly deposited black eggs was tested for randomness with the chi-square test ($P > 0.05$) for agreement with a Poisson series (Elliott 1977). Based on a contagious (clumped) dispersion model, we estimated the probable number of eggs spawned per day in 1996 within the spawning ground at rkm 215. The total number of eggs deposited was estimated based on the retransformed geometric mean of egg counts per sampler pad, the combined upper surface area of all buffer pad samplers, and the total substrate area covered by the sampling array. Mean width of the southern half of the river (25 m) for substrate area calculation was determined from taut rope-line measurements across 1995 transect lines A, S and V (Figure 2) when the river stage was 14.3 m above sea level at the gauging station at rkm 237; this was 1 m above the 10-year average for that station (U.S. Geological Survey, unpublished data).

Exploratory Egg Sampling at rkm 93

We deployed a second 12 × 4 array of samplers along the eastern side of the river at rkm 93 (Figure 1) beginning on 27 February 1996 when the river temperature was 20.5°C. The site at rkm 93 is the first river reach above the limit of tidal influence (rkm 73) that appeared to present an appropriate combination of emergent rock substrate, persistent seasonal eddies, reverse bottom currents, and depths approximating those at the spawning site at rkm 215. We hypothesized that spawning would not occur in tidal freshwater reaches, where the incoming tide wave tends to reduce or cancel river current, potentially precluding adequate oxygenation of eggs. We anticipated that the site at rkm 93 might offer an earlier spawning venue than the spawning site at rkm 215 because same-day water temperatures in spring are typically 1.5–3.0°C warmer at rkm 93 than at rkm 215. Samplers were inspected every third day until 1 April and approximately every fifth day thereafter until sampler removal on 11 April when the river temperature was 17.0°C.

Physical and Hydrological Characteristics

River currents and bottom topography at the study site at rkm 215 were profiled on 25 April 1995 with a four-beam acoustic Doppler profiler. One transverse profile was obtained across each transect in the sampler array at transects A–S. Two longitudinal profiles were also obtained parallel to each river bank between transects A and S. Substrate texture on the spawning site at rkm 215 was investigated and documented photographically along transect J via snorkeling during low-water conditions in November–December 1995 and in January and May–June 1996. For each 1995 egg collection, bottom depth was determined (nearest 0.5 m) with the sampler hauling line. In 1995, surface current was estimated (nearest 0.5 m/s) by timing the drift of floating objects along a marked 2-m section of the gunwale of our boat. Surface temperature was measured with a mercury bulb thermometer or portable Yellow Springs Instrument (YSI) meter. Conductivity and dissolved oxygen (DO) were determined by YSI meter. For each site-specific 1996 egg collection, we determined bottom depth (either by hauling-line length or by Humminbird depth sounder), surface current (to nearest 0.1 m/s by Gurley rotor-vane meter), and temperature (by YSI meter). In both years these physical measurements were also recorded once at the start of each sampling day, whether eggs were subsequently collected or not. However, time constraints precluded individual measurements for negative samplers.

Age-0 Gulf Sturgeon Sampling

We operationally defined age-0 Gulf sturgeon as postlarval fish less than 350 mm total length (TL). We defined juveniles as all postlarval fish less than 1,000 mm TL, thereby including age 0, age 1, and other sexually immature individuals up to age 5 or age 6. Larger fish (1,000–1,200 mm TL), though also sexually immature, migrate offshore in the company of adults and are commonly referred to as subadults. Upon completion of egg sampling in 1995 and 1996, sampling shifted to a multigear search for age-0 juveniles. The primary sampling gear was a 0.3-m (net mouth) epibenthic sled, which was adapted from the Woods Hole epibenthic sled (Hessler and Sanders 1967). The epibenthic sled, deployed in tows of 5–10-min duration, was equipped with 0.5-mm-mesh plankton netting in 1995 and 2.0-mm-mesh knotless nylon netting in 1996. Additionally, we trawled with a 3-m-footrope otter trawl made of 0.5-mm knotless nylon mesh. We also sampled occasionally by boat electrofishing. Trawling and electrofishing were conducted between rkm 0 and rkm 238, and a variety of biotopes was targeted.

Juvenile Sampling at the River Mouth, 1990–1993

Winter gill-net sampling (November–February) for juvenile Gulf sturgeon (ages 1–6) was conducted annually from 1988 to 1994 at the mouth of the Suwannee River, but data presented herein are confined to 1990–1993. Gear consisted of multiple 30.5–61.0-m-long monofilament gill nets (5–10 deployed per sampling day) with 13–75-mm-bar mesh set across river channels connecting with the open estuary. Sampling, usually scheduled for 2–3 d per week, was nonsystematic. It was designed to qualitatively map spatial and temporal patterns of occurrence and determine length frequencies among juveniles remaining at the mouth of the estuary over winter. Comparison of previous fork length (FL) data (Huff 1975) with our TL data was facilitated by use of Magnin's (1963) FL : TL conversion formula for *A. o. oxyrinchus.* Captures were grouped into 2-week intervals for comparative analysis.

Results

1995 Egg Sampling

Sampling on the 80-sampler grid design yielded 48 Gulf sturgeon eggs from collections on 3, 5, 7, 9, 11, and 13 April. The first eggs were collected 4 d after the new moon (30 March), when river temperature was 17.3°C. A final egg was collected on a redeployed sampler on 21 April after the original sampling grid had been dismantled; no additional eggs were found through 5 May. Excluding the egg collected on 21 April, eggs in 1995 came from 21 samples, representing 16 sampler positions (Figure 2). Five sampler positions yielded eggs on more than 1 d. Positive samplers contained 1–15 eggs each, although collections of a single egg predominated.

With one exception, all 1995 eggs were collected from the southern half of the river and were concentrated primarily (43 of 48 eggs) in an area extending from 150 m above to 415 m below the Alapaha Rise (transects E–M; Figure 2). This egg deposition area, centered on transects H and J, is characterized by a substrate of limestone bedrock overlain by a 0–10-cm-deep matrix of sand and abundant limestone gravel–cobble, subelliptical to subangular, and 2–10 cm in diameter, that is randomly distributed. Substrate on the northern side of the river is similar, but has less gravel–cobble, a much higher percentage of open sand sediment, and a muddier appearance. Live benthic arborescent algae were more abundant on the southern side of the river than on the northern side. Plant debris (plants, leaves, twigs, waterlogged Spanish moss) was negligible on samplers on the southern side of the river in 1995 and 1996 and during visual substrate inspection in November and December 1995. However, samplers on the opposite side of the river from the egg deposition area consistently collected light to heavy plant debris (leaves, twigs) in 1995. Water clarity was visibly reduced on the northern side of the river compared with the southern side (egg collection area) during underwater photography in January 1996. Except for the last egg collected, all 1995 eggs came from a narrow depth range (2.0–4.0 m; river stage, 14.0–14.6 m above sea level). Additional habitat variables measured concurrent with 3–13 April 1995 egg collections were as follows: estimated surface current velocity, 0.5–1.5 m/s (including reverse currents of 0.5–1.0 m/s); bottom temperature, 17.2–19.8°C (compared with 18.3–20.0°C for egg collections reported by Marchant and Shutters 1996); bottom conductivity, 88–109 μS; and bottom DO, 6.0–7.2 mg O_2/L. When the final egg was collected on 21 April, bottom temperature had risen to 21.5°C and bottom conductivity to 135 μS; bottom DO had fallen to 5.4 mg/L.

Most eggs collected from the samplers displayed clean chorions, free of attached debris. Chorions were still pliable upon adhesion to samplers as indicated by extensions drawn out from the egg surface upon contact with pad fibers. A small number of chorions had few to many adherent sand grains or embedded pieces of plant debris, suggesting either contact with the substrate or contact with suspended particles before attachment.

Samplers with eggs attached were from an area characterized both by high downstream subsurface current velocities (85–186 cm/s measured by Doppler device in 1995, 30–100 cm/s measured by Gurley meter in 1996) and by numerous eddies (as resolved by Doppler profiling; Figure 4A) compared with a general absence of eddies on the northern half of the river (Figure 4B). Notable among these is a large persistent eddy (Figure 2) observed during high waters (springs of 1995 and 1996), but absent during low water conditions (November 1995–January 1996 and August–October 1996). This eddy produced reverse bottom currents with velocities of 11–42 cm/s.

Of the 49 eggs collected in 1995, 10 were preserved to document the stage of development when collected, 2 were lost in transit, and 37 were transferred to the laboratory for incubation. When collected, most eggs were in early stages of development (1–8 blastomere stage) and were probably no more than 6–8 h old (Conte et al. 1988; Parauka et al. 1991). Early cleavage (black) eggs appear to have accounted for all eggs successfully hatched under laboratory incubation. Egg mortality due to fungal infection included most eggs collected in advanced developmental stages (i.e., yellow, neurulated embryo stage eggs) on 11 April. Fourteen eggs hatched successfully following 3–3.5 d of incubation at 17.5°C. Three yolk sac larvae died within 2 d, but the remaining larvae were reared for up to 17 d and were identified as Gulf sturgeon larvae.

1996 Egg Sampling

In all, 368 eggs were recorded in 1996 at rkm 215, of which 261 were black eggs, freshly deposited only hours before sampler inspection. Eggs were first observed on 26 March, 7 d after the new moon, at a water temperature of 14.9°C (having fallen from a 29 February temperature of 17.0°C following a series of cold fronts and heavy, cold spring rains). Subsequently, eggs were found on samplers on 29 and 30 March and 1, 2, and 4 April at temperatures of 17.0–20.0°C. Eggs were also found on sampler anchors, anchor lines, hauling lines, and Spanish moss and water-logged sticks that were fouled on samplers. After a 13-d hiatus, eggs were again found on 18 April (17 April spawn), coinciding with the April new moon, at a water temperature of 20°C. Exactly 100 eggs were observed during this second spawning round that ended 26 April. No spawning activity was detected

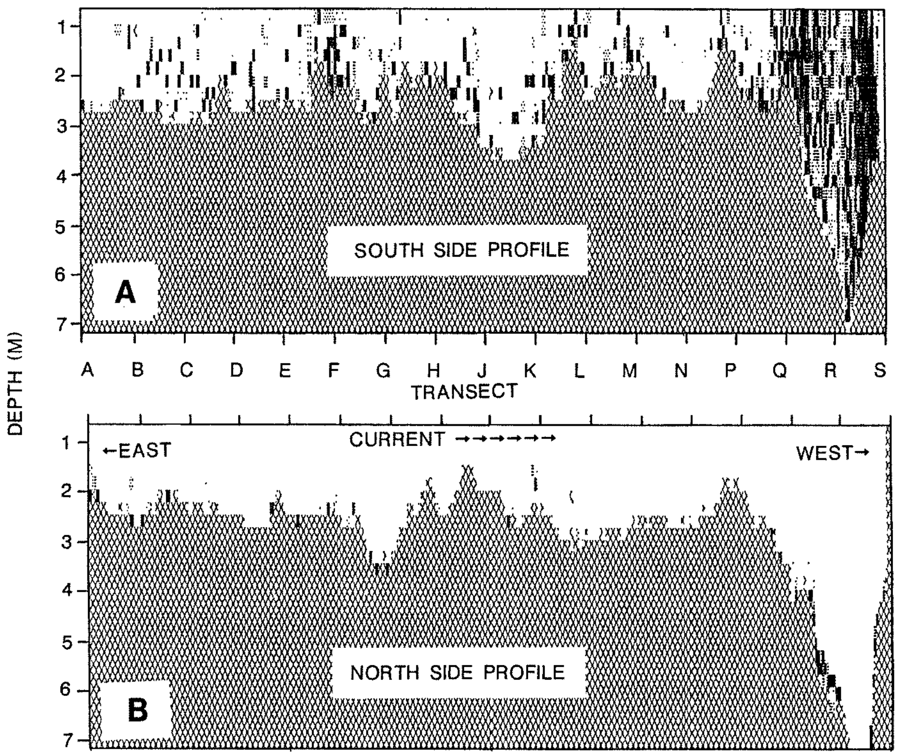

FIGURE 4.—Longitudinal (east to west) acoustic Doppler current profiles spanning sampling transects A through S (see Figure 2) at rkm 215 on 25 April 1995: **(A)** southern side of the river; **(B)** northern side of the river. Upper edge of cross-hatch pattern defines bottom topography. Dark patterning indicates current features (eddies) within the general background of strong laminar downstream flow (white areas). Mixed patterning indicates turbulent water. Current velocities have been truncated at ±20 cm/s to simplify the display. Vertical exaggeration equals 215:1.

thereafter through May 7 when samplers were removed. Eggs were concentrated within the same small area (~9,375 m^2; Figure 3) that yielded most eggs in 1995 (Figure 2). No eggs were observed on samplers at the exploratory site at rkm 93 through 11 April.

Physical measurements for the 26 March–19 April 1996 egg collections were as follows: bottom depth, 1.8–6.4 m; surface current velocity (Gurley meter), 0.2–1.2 m/s (including reverse currents of 0.1–0.2 m/s); bottom temperature, 17.0–20.9°C (except 14.9°C on 26 March); bottom conductivity, 51–101 μS; bottom DO, 5.4–7.1 mg/L. Temperature, conductivity, and DO were relatively stable throughout the spawning period. However, after 21 April, near the end of 1996 spawning activity, the hydrological variables began to change rapidly. When the last eggs were collected on 26 April bottom temperature had risen to 22.7°C, conductivity to 129 μS; and DO had fallen as low as 4.1 mg/L. At rkm 93, where no eggs were collected, the following ranges of hydrological measurements on the bottom (27 February–11 April) were recorded: temperature, 15.0–20.5°C; conductivity, 81–250 μS; and DO, 5.4–8.2 mg/L.

Estimates of new black eggs spawned per individual spawning event at rkm 215 were 404,600 (29–30 March), 565,200 (1 April), and 711,000 (18 April). This approximates the fecundity range (275,000–475,000 eggs) reported for individual large female Gulf sturgeon (Chapman et al. 1993). Under the conditions of strong surface current prevailing at rkm 215, we anticipated very broad and essentially random dispersion of eggs among our regularly spaced samplers. Instead, chi-square test for agreement of sampler egg counts with a Poisson series was rejected at the 95% probability level, indicating nonrandom dispersion of eggs. Calculated values of normal variable *d* (Elliott 1977) for 1996 data (3 days) indicate that newly spawned black eggs were highly contagiously distributed.

TABLE 1.—Synopsis of data for captured or visually sighted (with asterisks) riverine juvenile (≤450 mm total length, TL) Gulf sturgeon in the Suwannee River, 1989–1996 (refer also to Figure 1). Captures from below river kilometer (rkm) 10 and hatchery fish recaptures have been excluded.

Location (rkm)	Date	Water temperature (°C)	Depth (m)	TL (mm)	Weight (g)	Habitat type[a]
Age-0, ≤350 mm TL						
93.0	5 May 1995	23.2	3.0	82	1.5	SND
207.0	7 Jul 1995	28.0	1.5	94	2.6	N
33.0	21 Jun 1996	26.9	3.8	115	1.5	SCD
190.0	7 Sep 1993	24.5	<1.0	251	48.8	SC
55.5	17 Jun 1993	25.4	7.5	282	75.5	
215.0	29 Jun 1993		<1.0	283	82.6	SC
190.0	7 Sep 1993	24.5	<1.0	285	68.8	SC
213.5	23 May 1995	25.5	2.0	290	75.0	SCW
213.5*	23 May 1995	25.5	<2.0	~300		SCW
189.0*	31 May 1995	23.0	1.0	~300		SNW
40.0	3 Jun 1995	23.9	6.0	301	88.5	
215.1	3 Dec 1991	19.0	5.5	306	85.0	SN
215.0	29 Jun 1993		<1.0	311	92.0	SC
215.0	7 Jun 1993		<1.0	311	114.0	SC
237.5	15 Jan 1992	14.2	1.0	313	76.5	S
70.6	3 Jun 1993	25.5	1.0	326	110.2	
212.0	25 May 1995	23.0	<3.0	340	122.0	SCW
184.5*	31 May 1995	23.0	1.0	~350		SNW
Probable age-1+ juveniles, 351–450 mm TL						
221.0	3 Aug 1993			355	130	
55.5	21 Jul 1993			361	172	
190.0	7 Sep 1993	24.5	<1.0	372	207	SC
55.5	1 Sep 1992			389	210	
37.0	18 Jan 1996			394	205	
221.0	2 Jul 1992			395	214	
200.2	2 Sep 1992			412	232	
12.0	22 Jan 1996			412	215	
71.0	18 Nov 1993			418	202	
221.0	28 Aug 1990			422	270	
37.0	17 Jan 1996			425	265	
93.2	8 Nov 1993			435	290	
40.5	8 Dec 1993			435	270	
37.0	18 Jan 1996			442	270	
200.2	29 Jun 1989			449	400	
55.5	6 Oct 1992			449	290	

[a] Habitat key: C = midchannel, N = nearshore, S = sandbar, W = fine white sand, D = coarse dark sand.

1995–1996 Riverine Juvenile Sampling

Trawling, electrofishing, gillnetting, and visual surveys in 1995–1996, combined with 1989–1994 results, produced 34 Gulf sturgeon juveniles (ages 0 and 1, ≤450 mm TL) from Suwannee River freshwater (Table 1). Specimens of 82, 94, and 115 mm TL captured at rkm 93, 207, and 33 (Table 1) are the first documented captures of juveniles smaller than 150 mm TL and less than 3 months of age from any river. They provide the first evidence of early juvenile habitat requirements.

River Mouth Juvenile Sampling

Gill nets fished in the estuarine mouth of the Suwannee River (rkm 0–2.5) in November–February (1990–1993) captured 461 wild Gulf sturgeon juveniles ranging from 339 to 988 mm TL (Figure 5A). Tagged wild juveniles recaptured within and between winter sampling seasons were excluded from the database and are not represented in Figure 5. Also excluded were 30 winter river-mouth recaptures from 1,192 hatchery-reared juvenile sturgeon (identified by individual passive integrated transponder, PIT, tags) released in the Suwannee River in 1992 by the U.S. Fish and Wildlife Service (J. Clugston, unpublished data). A plot of length frequencies for the four consecutive winter sampling periods combined (1990–1993) revealed a well-defined mode of 400 mm TL (Figure 5A), attributable predominantly to age-1 juveniles recently arrived from upriver in late January to mid-February of each year (Figure

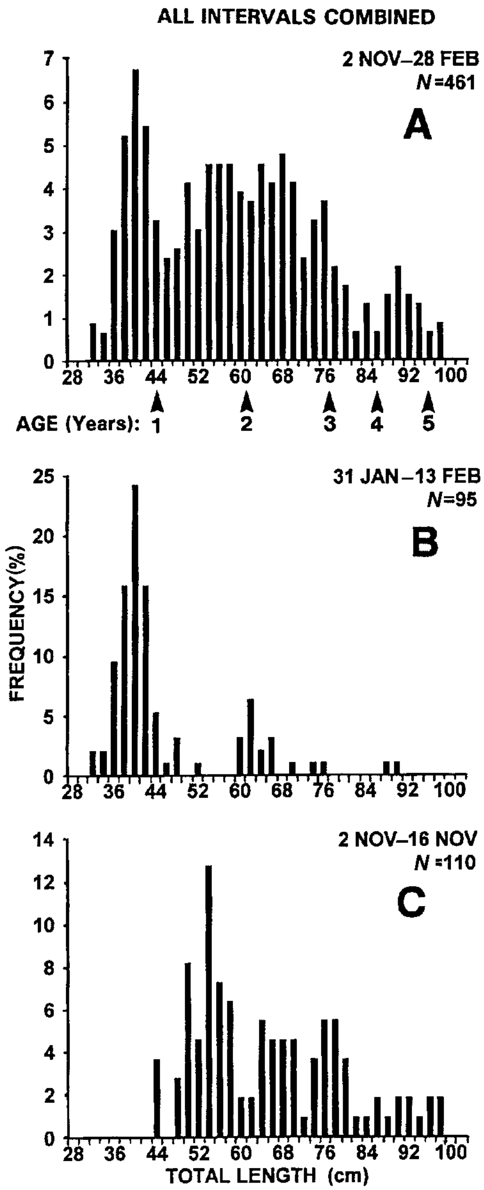

FIGURE 5.—Frequency distribution (by total length [TL], grouped in intervals of 2.0 cm) of juvenile Gulf sturgeon captured in gill nets at the Suwannee River mouth (West Pass) during winter (Nov–Feb), 1990–1993. Fish captures were analyzed by 2-week intervals: **(A)** plot for all 2-week intervals combined, 2 November through 28 February; **(B)** plot for 2-week interval, 31 January through 13 February (a subset of A); **(C)** plot for of 2-week interval, 2 November through 16 December (a second subset of A). Arrows below *x*-axis in A denote mean estimated size-at-age (TL) for fish at ages 1–5, as derived from Huff's (1975) regression formula for fork length versus age, FL (mm) = 369.2326 $age^{0.5284}$, converted to TL by using the formula of Magnin (1963) for *A. o. oxyrinchus*: TL (mm) = FL(1.10) + 17.1.

5B, a 2-week subset of Figure 5A). This age-1 mode is absent from earlier 2-week sampling intervals, including that period corresponding to peak emigration of older juveniles and adults in early November (Figure 5C, a second 2-week subset of Figure 5A).

Discussion

Before 1995, only six Gulf sturgeon eggs had been collected from any river, all from 1993 and 1994 sampling in the Suwannee River (Marchant and Shutters 1996). Four of these eggs were from the site at rkm 215, which suggested this was a probable spawning site. Our subsequent collection of substantial numbers of eggs there in 1995 and 1996 confirms that rkm 215 is a Gulf sturgeon spawning site used each year. To date this is the only well-documented Gulf sturgeon spawning site in the Suwannee River, but single eggs collected at rkm 201 and rkm 221 suggest there may be others and indicate a need for equivalent sampling effort at other potential spawning sites.

A geological discontinuity, the Cody Scarp, separates two major physiographic regions in north Florida, the Northern Highlands and the Gulf Coast Lowlands (Mattson et al. 1995). Although the scarp is readily passable by Gulf sturgeon, it may nonetheless impose an upstream geological–physiological boundary on suitable spawning habitat at about rkm 230. Above the scarp the river is dominated by surface water runoff and characterized by highly variable flow rates and turbid, acidic, low-conductivity water. Below the Cody Scarp, spring water input produces a more even flow rate and less variable hydrological conditions (Mattson et al. 1995). Rapid, unpredictable variations in water conditions, such as temperature, conductivity, hardness (Ca^{++} ion content), pH, and dissolved oxygen are potentially deleterious to developing Gulf sturgeon embryos. Moreover, a predictable range in Ca^{++} ion concentration may be essential to gamete success (Cherr and Clark 1985).

The availability of bedrock, plus clean gravel–cobble substrate for egg adhesion and sheltering of developing larvae, is probably another critical geological requirement for early life history stages. Bedrock underlying shallow areas with consistently high current velocities promotes substrate surface mobility, resulting in clean sediment and scoured gravel–cobble. Exposed bedrock, not heavily buried beneath sand, occurs only in rare patches below rkm 230. Riverbed topography also appears to play a role in determination of sturgeon spawning sites. Underwater topography determines the location of eddy fields, like that coinciding with the spawning site at rkm 215. Eddy fields cause diminished or reversed bottom currents in areas otherwise dominated by strong laminar currents. Thus, they may be important in maintaining gametes in close conjunction, thereby promoting fertilization and diminution of gamete wastage. They probably also facilitate rapid sinking and adhesion of eggs to the substrate. The discharge of the Alapaha Rise adjacent to the spawning site at rkm 215 may function to generate a persistent eddy field critical to spawning behavior. The eddy zone coinciding with the egg site at rkm 215 occupies the side of the river with the strongest downstream subsurface current velocities. Strong, persistent flow has been suggested as an important determinant of spawning in other sturgeon species (Votinov and Kasyanov 1978; Kieffer and Kynard 1996; Parsley et al. 1993; Auer 1996). The confluences of other major tributaries with the Suwannee River main stem (e.g., the Withlacoochee River mouth) suggest additional candidates as spawning sites.

Geological features in conjunction with seasonal water levels may also impose limits on habitats available to age-0 Gulf sturgeon in most years. Over much of the summer, the lower Alapaha River courses underground, and the upper Suwannee River is not passable at Big Shoals due to low water levels.

At the outset of this study, strong clumping of eggs on samplers was not anticipated because sturgeons have been characterized as broadcast spawners (Vladykov and Greeley 1963; Parsley et al. 1993). Additionally, hatchery observations of stripped or extracted eggs of white sturgeon *A. transmontanus* (Conte et al. 1988) suggested that fertilized eggs were not immediately adhesive. However, the delay may be an artifact of laboratory-induced ovulation and physical removal of eggs. Also based on observations of white sturgeon, Cherr and Clark (1985) generalized that sturgeons release eggs over large areas of river bottom. However, at rkm 215 in the Suwannee River, we found that spawning activity in Gulf sturgeon appears to be confined to a very small area (Figure 3). In 1996, 93% of the eggs observed came from transects XG–E4 (Figure 3), representing an area no larger than 9,375 m^2. From the highly contagious distribution of eggs recovered, we inferred that eggs spawned in the wild typically sink and stick to the substrate almost immediately upon extrusion, rather than drifting some appreciable distance and dispersing downstream in midwater before adhering (Parsley et al. 1993). Although the contagion could have resulted from eddy concentration of drifting eggs, rapid adhesion tends to be confirmed by the general lack of attached debris on the chorions of eggs found on buffer pads and by groups of up to 63 eggs found on individual samplers. We lack in situ observational data on whether Gulf sturgeon spawn just above the substrate or higher in the water column.

The uniformity of developmental stage observed among eggs collected on each day strongly suggests that a single spawning bout by a single female occurred on each day eggs were collected. An exception occurred on 1 April 1996, when two distinct batches of new eggs differing in developmental stage were found, suggesting two spawning events separated by several hours. It appears that as many as 10 females separately used the site at rkm 215 on individual days during the first spawning round in 1996. Each female appears to depart immediately after spawning, based on separate empirical observations. Thus, in related research, we biopsied a female (1,835 mm TL, 43.0 kg) captured in November 1995; the biopsied ova were white and 1.5–2.0 mm in diameter. The same female was relocated acoustically in 1996 at the center of the egg deposition area on 26 March and had probably spawned. It was detected only on that day and not thereafter. The occurrence of a second round of spawning in 1996 after a hiatus of 13 d also indicates use of the site by a second group of ripe females.

Egg loss from samplers is a confounding variable in resolving spawning activity. From daily sampling in 1996 (28 March–2 April) we found that the majority of 0-d-old black eggs were gone from sampler pads reexamined 24 h later, before reaching the 1-d-old brown stage. Because individual eggs were typically firmly attached to buffer pads (pad fibers embedded in coalesced chorion), we hypothesize that egg loss before hatching is generally not attributable to current scour, but to predation by fishes (e.g., catfishes *Ictalurus* spp. and blackbanded darters *Percina nigrofasciata*) or large aquatic insect larvae. Zhong-Ling and Zhao-Yan (1991) reported that six benthic fish species (four cyprinids, two catfishes) fed on eggs of *A. sinensis* in the Yangtze River, China. Egg loss can also occur due to infections; we noted a small number of fungus-infected or shriveled eggs on 2 April 1996. Such nonviable eggs may be readily shed from samplers.

Spawning activity in 1995 began 4 d after the

30 March new moon at water temperatures of 17.3–17.5°C. In 1996, the first eggs were observed 7 d after the 26 March new moon at a water temperature of 14.9°C. A second round of spawning in 1996 coincided with the new moon in April after a 13-d spawning hiatus. Based on comparison with size-at-age data for cultured sturgeon (Mason et al. 1992), the 82-mm-TL juvenile from rkm 93 was approximately 60 d old when captured, indicating a probable hatch date of 3 March 1995 (prior to initiation of our egg sampling that year). Although we did not detect spawning at rkm 215 until early April 1995, an earlier spawning appears to have taken place approximately coincident with the 1 March 1995 new moon. Thus, spawning activity appears to be coordinated with lunar phase, and the initiation of spawning each spring may be predicted to within a few days.

We pursued the hypothesis of earlier spawning downstream in 1996 but failed to collect eggs at the sampler transect site at rkm 93. This site appears to have suitable substrate and current attributes but higher conductivities (typically >200 μS) than at rkm 215. Due to very low precipitation over the period of November 1995–March 1996, the Suwannee River was shallow in early 1996; temperatures were thereby influenced by warm spring water. Water temperatures rose rapidly at rkm 93 to 20.5°C by 27 February. Thus, conditions were atypical and perhaps unfavorable (too warm too early) for downstream spawning in 1996 even before onset of adult Gulf sturgeon immigration on 22 February (K. Sulak, unpublished data).

The trigger for initial upstream spawning migration from estuarine staging areas by Gulf sturgeon may be a combination of factors. These could include a critical minimum water temperature of 16.0–19.0°C (Foster and Clugston 1997), semimonthly lunar high water at the river mouth, and maximum darkness accompanying new moon to first-quarter moon. Water temperature appears to be a primary predictor of egg deposition in white sturgeon (McCabe and Tracy 1994). Depending on volume of river outflow and height of incoming tide, tidal high water at new moon reduces or negates river current in the lower 60–70 km of the Suwannee River, potentially facilitating upstream migration to spawning sites. Once initiated, spawning activity in 1995 occurred at rkm 215 from 3 to 13 April and in 1996 from 26 March to 4 April and from 17 to 26 April, based on collection of newly spawned black eggs on consecutive sampling days. In 1995, the limited number of samplers deployed in the center of the egg deposition area produced no eggs on 15, 17, or 19 April (water temperature = 22.0°C) or from 23 April to 5 May (water temperature = 23.0°C). The single egg collected 21 April at 21.0°C appeared normal but remained undeveloped over 5 d of laboratory incubation, so it was probably infertile. Temperatures approaching the critical lethal limit of 25°C for embryos (Chapman and Carr 1995) may dictate cessation of Gulf sturgeon spawning. Three 1–2-d-old larvae (yolk sac embryos) from the Apalachicola River (Wooley et al. 1982) were collected at a maximum temperature of 23.9°C.

Temperatures for all but one egg deposition event at rkm 215 in 1995 and 1996 were 17–22°C. The critical temperature cue required to trigger physiological processes preparatory to reproduction (hormonal–gonadal activity) may be lower. Cessation of spawning probably corresponds with a critical maximum temperature at the spawning site or with a rapid rise in ambient water temperature. In years with extended cool conditions in spring, the thermal window for spawning may extend through two (as in 1996) or even three lunar cycles. The spring immigration of large adults does not cease until the first week of May (J. Clugston, unpublished data).

A substrate matrix of clean gravel–cobble on clean sand over a horizontal bedrock platform coincides with the spawning site at rkm 215 (Figure 2) and may represent benthic habitat suitable for spawning and subsequent larval development. The pebbly gravel is probably mobile under high flow conditions, assuring clean scoured surfaces suitable for egg adhesion. Gravel–cobble substrate has similarly been indicated as spawning habitat in other sturgeon species. Kieffer and Kynard (1996) state that gravel substrate is used for spawning by the shortnose sturgeon *A. brevirostrum.* Clean gravel added to a Wisconsin river was used as spawning substrate by lake sturgeon *A. fulvescens* (Folz and Meyers 1985). For *A. sinensis*, Zhong-Ling and Zhao-Yan (1991) reported a spawning ground substrate of gravel bars and rocks 4–10 cm in diameter, which is similar to gravel size found at the spawning site at rkm 215. Parsley et al. (1993) reported that white sturgeon eggs were collected mostly over cobble (6.4–25.0 cm) and boulder (25.0–400 cm) substrates in the Columbia River.

We failed to collect eggs, wild yolk sac larvae, or early postlarvae in plankton nets in 1995 at rkm 215, and so did Huff (1975) in earlier plankton netting at 32 sites between rkm 26 and 253. The behavior of early larvae and the nature of egg collection site substrate (gravel) may account for the general failure of plankton nets and benthic traps to capture larvae. Early larvae are benthic, negatively phototactic, strongly thigmotactic, and largely sedentary, based on our laboratory observations. The cryptic larvae probably take refuge in the gravel substrate, rendering most types of fixed or towed gear ineffective in collecting them. In 1996, we incidentally collected a single newly hatched larva adhering to the shaft of a sampler anchor. Except for this specimen and three yolk sac larvae 1–3 d old collected in the Apalachicola River (Wooley et al. 1982), the larval and early postlarval stages of Gulf sturgeon remain undiscovered and their habitats undefined. Pavlov (1994) hypothesized rapid downstream dispersal for larvae and developing juveniles. Our captures of juveniles (82 and 115 mm TL) well downstream (rkm 93 and rkm 33) of the known spawning area tend to support Pavlov's hypothesis. Recent data on the white sturgeon in the lower Columbia River (McCabe and Tracy 1994) also agree with Pavlov's model for anadromous fishes. Juvenile white sturgeon habitat in that river is more than 50 km downstream of the region of egg deposition. However, our July capture of a 94-mm individual far upstream (Suwannee River rkm 207) indicates that the distribution pattern of early juvenile Gulf sturgeon is not so simply explained.

Our three smallest age-0 fish (82–115 mm TL) are by far the smallest postlarval Gulf sturgeon ever reported from any river. Juveniles 450 mm or less have been infrequent in our previous samples, despite the extensive use of gill nets with mesh as small as 13 mm (bar measurement). Seven years of intensive gill net sampling and limited electrofishing upstream of rkm 30 in our study and by Clugston et al. (1995) yielded 11 young Gulf sturgeon (251–372 mm TL); these are the only documented records of early juveniles from Suwannee River freshwater, aside from one recent report (Carr et al. 1996). Juveniles between 251 and 372 mm TL are probably at least 6–12 months old based on size-at-age data for laboratory-cultured (Mason et al. 1992) and wild fish (Huff 1975).

Estuarine-phase juveniles (339–988 mm TL) were common in our winter gill-net samples (November–February 1990–1993), at the mouth of the Suwannee (Figure 5A). However, juveniles 450 mm TL or smaller (the smallest gill-net size mode, <12 months old) were rare in the estuary at all times (e.g., Figures 5A, C), except during the first half of February (Figure 5B). This indicates that age-0 juveniles do not emigrate to the estuary from late October through early November in the company of larger Gulf sturgeon. Instead, we hypothesize that age-0 fish remain in riverine habitats through January and arrive in the estuary in February as age-1 fish (Figure 5B), whereas larger fish (≥age-2) arrive 3 months earlier (Figure 5C). Negative data from previous estuarine sampling during other months support this inference. Huff (1975) caught 632 specimens in 125-mm-bar-mesh gill nets in West Pass at the Suwannee River mouth in March–May and October–December 1973, but only a single fish less than 500 mm fork length (FL) was captured (380 mm FL = ~438 mm TL). From the same area, Huff (1975, Figure 20) also caught 106 specimens in trammel nets (smallest mesh, 28 mm bar) in spring 1973, but only a few were less than 420 mm FL (484 mm TL). The smallest was about 260 mm FL (~300 mm TL); their mean size was approximately 550 mm FL (634 mm TL). McCabe and Tracy (1994) found a similar absence of age-0 white sturgeon from the Columbia River estuary. However, our gill-net data for Gulf sturgeon probably underrepresented fish 450 mm TL or less and must be qualified accordingly. Such small fish may be more vulnerable to capture in bottom trawls (McCabe and Tracy 1994) with fine-mesh liners or in sled trawls, neither of which has been used extensively at the Suwannee River mouth. Data is limited regarding the general location and habitat of age-1 Gulf sturgeon juveniles following the overwintering period (November–February). But our captures of juveniles 350–450 mm TL (Table 1) suggests these and larger age-1 fish move upstream and redisperse widely in the Suwannee River.

Resolution of dispersal patterns and seasonal occurrence patterns for riverine age-0 juveniles (251–350 mm TL; Table 1) is equivocal based on our collections and those of Carr et al. (1996). Our May and June captures of 11 juveniles between 282 and 350 mm TL in 1993 and 1995 (Table 1) are particularly perplexing. These fish, equivalent in size to 6–10-month-old fish (Huff 1975; Mason et al. 1992), suggest three alternatives: (1) they represent greatly oversized age-0 fish from the same year's spring spawning, (2) they represent considerably undersized age-1 riverine juveniles from the previous spring's spawning (1992 and 1994), or (3) they represent appropriate-size progeny from secondary fall spawnings in 1992 and 1994. Alternatives 1 and 2 seem very improbable based on our size-at-age growth curves for juveniles (K. Sulak, unpublished data). Although alternative 3, fall spawning, has not previously been suggested for Gulf sturgeon, size-at-age data support that alternative. Mature fish entering the Suwannee River too late in spring may be prevented from spawning by high water temperatures. Such fish may wait until October or November to spawn in years offering a long, cool fall that presents a suitable thermal window (17–22°). In several years, during the fall, we have captured a small number of gravid females carrying fully mature black ova (2.4–2.5 mm diameter) and running-ripe males with motile sperm.

Our capture records indicate that age-0 and age-1 Gulf sturgeon prefer open sand shoals. Clugston et al. (1995) reported the first captures of young-of-the-year Gulf sturgeon from 1991 sampling on the extensive sandbar at rkm 213, the same sand shoal from which Carr et al. (1996) subsequently reported additional 1993 captures. Further, juveniles from this same area include a specimen less than 350 mm TL reported by Florida Game and Fresh Water Fish Commission biologists (personal communication to J. P. Clugston) and a specimen about 150–200 mm TL reported by the Suwannee River Water Management District (R. Mattson, personal communication). Localities for our 28 captures and 3 visual records of juveniles 450 mm TL or less span over two-thirds of the Suwannee River main stem (Table 1). Age-0 fish also inhabit tributaries. Huff (1975; and personal communication) reported a 234-mm (standard length) specimen in the Santa Fe River, 19 rkm upstream of the Suwannee River confluence at rkm 110. If juveniles typically remain in freshwater until 350–450 mm TL and occur well upstream over a range of sizes, then Pavlov's (1994) model of progressive downstream migration may not satisfactorily explain the distribution of age-0 to age-1 Gulf sturgeon.

Carr et al. (1996) stated that river areas adjacent to springs are probable Gulf sturgeon spawning sites and that spring areas provide suitable habitat for age-0 juveniles. This implies that developing fish remain in or close to springs. However, there is little evidence from their report, previous investigations, or our study to support such a general statement. Juveniles reported by Carr et al. (1996) did not come from the immediate vicinity of the Alapaha Rise (rkm 215), the nearest major spring, but from a shoal 2 km downstream. Moreover, although located immediately adjacent to our spawning site, the Alapaha Rise is very atypical compared with most magnitude-one Florida springs (Rosenau et al. 1978). Other major springs discharging into the Suwannee River have crystal-clear (0–5 platinum cobalt color units) Florida aquifer groundwater, which exhibits relatively high conductivity (257–413 μS) and stable warm temperatures (21.0–23.5°C) year-round. The Alapaha Rise is very turbid and tannic (60 platinum cobalt units; Rosenau et al. 1978) and, as measured in our study, displays variable conductivity (50–225 μS) and seasonally variable temperatures (13.0–21.0°C) and DO levels (0.5–4.6 mg/L; April 1996–February 1997). It discharges 2–6 times as much water (17 m^3/s) as other major Suwannee River drainage springs (2.8–10 m^3/s). The nearest large springs with typical Florida aquifer characteristics are Falmouth Spring, 11 rkm downstream, and Suwannee Springs, 22 rkm upstream. Despite considerable sampling effort with multiple gear types, we have neither collected nor observed any juvenile Gulf sturgeon at the spawning site at rkm 215 nor in close proximity to any typical spring. However, with more than 50 sizable springs along the 250-rkm main stem of the Suwannee River, almost any identifiable spawning site should lie within 5–10 rkm of a named spring, which occur on average every 5 rkm.

A positive association with spring-water habitat also seems very improbable for early life history stages of Gulf sturgeon, based on water chemistry. Florida spring water, typically very low in oxygen tensions (0–4 mg/L; Rosenau et al. 1978), is probably inhospitable to early juveniles. Jenkins et al. (1995) demonstrated that juvenile shortnose sturgeon (age 11–330 d) begin to encounter mortality when held at DO concentrations below 3.5 mg/L in the laboratory. Young fish (age 64 d) were particularly susceptible, exhibiting 86% mortality when held for 6 h at 2.5 mg DO/L.

By providing the appropriate ionic milieu for gamete function, certain springs, rises, or tributaries may play a positive role in delineating sections of the river suitable for spawning. In white sturgeon, Ca^{++} ions appear essential to egg jelly coat hydration, which promotes adhesiveness for attachment to the substrate (Cherr and Clark 1985). Calcium ions and an alkaline pH also play an important role in the sperm acrosome reaction, that is, discharge of acrosome during egg fertilization (Cherr and Clark 1985). Huff (1975) documented a substantial input of $CaCO_3$ (as a doubling of Suwannee River water hardness) at the Alapaha River–Rise outflow coincident with our spawning site at rkm 215. Hardness is typically much lower above the Alapaha Rise, and pH is typically acidic (5.2–7.2 upstream versus 6.5–8.5 below; Huff 1975; Mattson et al. 1995). Alternatively, high

Ca^{++} ion concentration downstream (e.g., rkm 93) may preclude spawning. Resolution of physical, hydrological, and chemical requirements for Gulf sturgeon spawning and juvenile nursery habitats will require more extensive collections and more systematically derived and tested habitat data than are currently available. Beyond an apparent affinity for sand shoals among juvenile Gulf sturgeon, the biotopes that serve as nursery habitat remain unresolved, as do the physical and habitat conditions essential for early development.

Conclusions

Conclusions concerning Gulf sturgeon spawning are as follows. (1) Onset of spawning at rkm 215 in the spring of 1995 and 1996 took place 4–7 d after the new moon, once water temperature had risen to 17.0°C. (2) Spawning lasted for 10–11 d. (3) A second 10-d round of spawning occurred on the subsequent new moon in 1996, when water temperatures remained below 22°C. (4) Eggs at rkm 215 were contagiously distributed and deposited within a small area on the southern half of the river characterized by numerous eddies. (5) Spawning ground substrate consisted of a bedrock platform covered with clean gravel on a thin bed of fine sand. (6) Ranges in physical parameters that appear to bracket the main spawning period are temperature, 17–19°C; conductivity, 50–100 μS; DO, $>$6.0 mg/L. Values for these variables change rapidly at the end of the spawning period.

Conclusions regarding juvenile Gulf sturgeon are as follows: (1) Age-0 and age-1 Gulf sturgeon occurred between rkm 12 and rkm 238. (2) They were found primarily on shallow (typically $<$4-m) sandbars and rippled sand shoals; all specimens came from open-river biotope, and none came from vegetated shoreline or rocky biotope. (3) All collections came from tannic main-stem river water; none came from spring mouths or immediately adjacent habitat. (4) Juveniles 450 mm TL or less were collected in freshwater from May through January; those 350–450 mm TL appeared at the river mouth estuary predominantly in early February. (5) Juveniles up to 1,000 mm TL overwintered at the river mouth and did not appear to migrate offshore with larger subadults and adults.

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